Vol. IX. *November, 1905.* *No. 6*

BIOLOGICAL BULLETIN

THE DISTRIBUTION OF TRACHEÆ IN THE NYMPH OF PLATHEMIS LYDIA.

G. G. SCOTT.

The Odonata are regarded as among the most highly organized of insects. In fossil dragon flies found in the Tertiary are indications of high specialization. Dragon flies are especially adapted to swift flight. For this purpose they are supplied with broad wings and powerful muscles to work them. There is consequently a great need for a plentiful supply of oxygen. This is supplied to every tissue in all parts of the body by the tracheal system. On this account a study of the tracheal system is of interest and importance.

The late Professor James I. Peck, of Williams College, suggested to the writer in 1898 that he make a study of the distribution of tracheæ in the nymph of a dragon fly found near Williamstown, Mass. It is from notes and drawings made at that time that the present paper is written. The forms found were identified by Professor James Needham as *Plathemis trimaculata,* which name I am informed has since been changed to *Plathemis lydia.* Lubbock says that the larval tracheæ of insects are more generalized and represent more nearly the original type than those of the adult. The results of this investigation show clearly that on the other hand we have in the nymph of *Plathemis lydia* a very special and complex distribution of tracheæ in some respects especially adapted to aquatic larval life and changing to simpler conditions in the adult. Lubbock states that the distribution of the tracheæ depends on the size and shape of organs. Yet in the nymph of *Plathemis lydia* there are certain complexities that are not thus easily explained. For example the tracheæ

of one side cross over and fuse with the tracheæ of the opposite

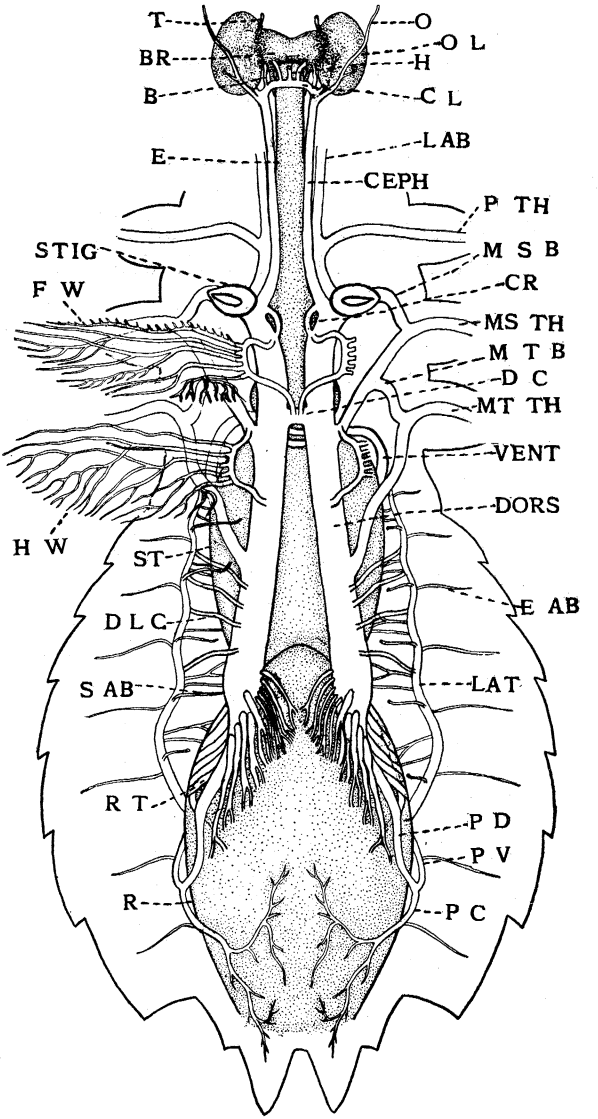

FIG. 1.

side. The distribution in the main however follows the contour of organs or axis in parts.

Plathemis lydia belongs to the family Libellulidæ of the order

Odonata. The Libellulidæ are among the most highly organized of the Odonata. As far as the tracheal system is concerned *Plathemis lydia* is well classified. The nymph is aquatic, inhabiting the muddy bottoms of quiet pools. It has a swift darting motion when disturbed, caused by expelling water from the rectum. The average length of those studied was 23 mm., the width 7 mm. The head is marked by the large eyes at the upper outer angles ; a single pair of short antennæ extend from below and between the eyes. The prominent mask, a modified labium, covers the mouth parts. There are three pairs of legs, all attached to the thorax, which also bears dorsally two pairs of short functionless wings. Anterior to these is a single pair of prothoracic stigmata, functionless also. On the abdominal segments are found seven pairs of functionless stigmata. Internally the alimentary canal extends from mouth to anus and consists of esophagus (Fig. 1, *E*), stomach (Fig. 1, *ST*), intestine and rectum (Fig. 1, *R*). At the junction of the stomach with the intestine are the malpighian tubules. On the dorsal face of the gut over the rectum and stomach is the slightly lobed blood vessel. On either side of this and somewhat posteriorly are the immature reproductive organs.

Ventral to the gut is the chain of seven abdominal ganglia (Fig. 2) the posterior being the largest. The ganglia are connected by nerve cords to each other and by the same method anteriorly with the thoracic ganglia (Fig. 2). There are three of these not fused, the meta- and mesothoracic being nearer together than the meso- and prothoracic. The prothoracic ganglion connects by nerve cords with the subesophageal ganglion and this by the esophageal ring with the dorsally lying brain (Fig. 1, *br*). On the upper outer sides of the brain are the large optic lobes.

It is the tracheal distribution to the foregoing parts that I have worked out and also the connections and interconnections of the tracheæ.

Methods.

The nymph was placed in a strong solution of glycerine in a watch glass and the dissections made with small scissors and needles sharpened down to cutting edges. Most of the work was done with a dissecting microscope. In the glycerine solu-

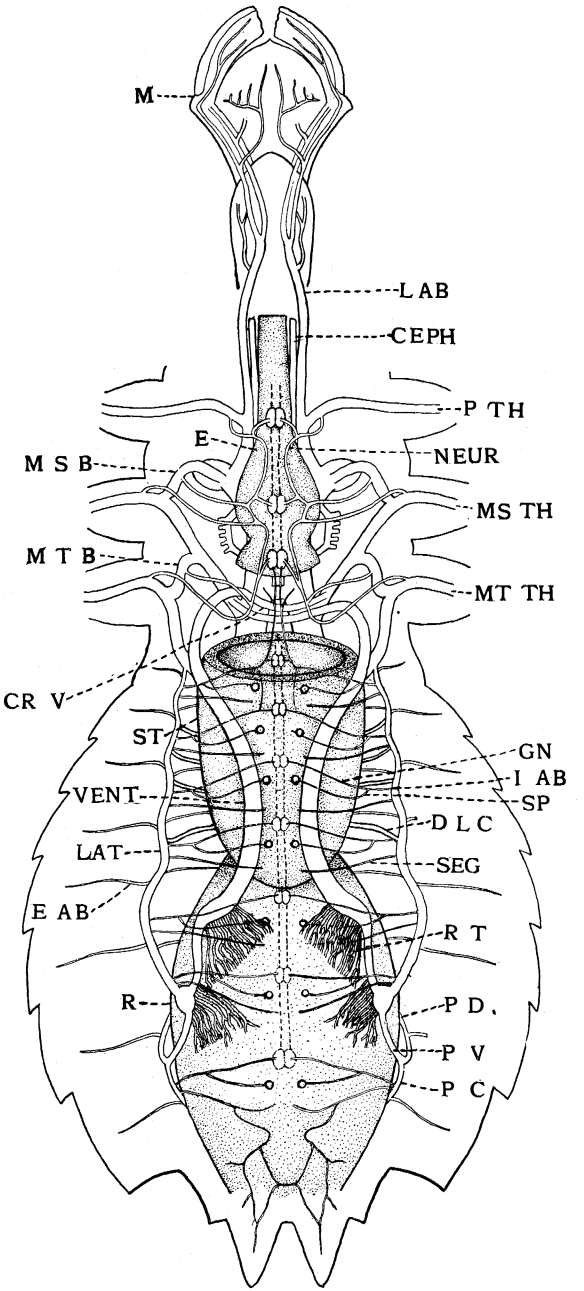
M
LAB
CEPH
P TH
E
NEUR
M S B
MS TH
M T B
MT TH
CR V
ST
GN
I AB
VENT
SP
D L C
LAT
SEG
E AB
R T
R
P D.
P V
P C

FIG. 2.

tion the tracheæ appeared as silvery white tubes. Some of the more minute points were worked out teasing with needles under the lower powers of the compound microscope. Glycerine mounts were easily made and studied.

Tracheal Distribution.

According to Packard '98 the tracheal system of *Plathemis lydia* belongs to the peripneustic type in which the prothoracic and abdominal stigmata are present though not functional during the greater part of the larval life. This type is intermediate between the holopneustic or open type and the apneustic or closed type.

The Dorsals. — The tracheal system is most conveniently understood by considering first those that lie dorsally, then those that are ventral and those that run laterally. In connection with each of these three systems there will be given an account of their principal branches. The connections of each of the others will be described. The stigmata found dorsally between the pro- and mesothorax will serve as a convenient starting point. From each of the stigmata (Fig. 1, *STIG*) the two largest tracheal tubes, the dorsal tracheæ (Fig. 1, *DORS*) extend posteriorly, diverging slightly to the sides of the rectum. There is a small crescent-shaped trachea (Fig. 1, *CR*) arising from the inner face of the dorsals at the stigmata and joining the dorsals again a short distance behind.

About one fifth of their distance back of the stigmata the dorsals are connected by a trachea of about one half their own diameter (Fig. 1, *D C*). The trachea to the mesothoracic leg (Fig. 1, *MS TH*) arises from the dorsal just back of the above mentioned connective. It receives a branch (Fig. 1, *M S B*) from the dorsal at the stigmata. The tracheæ to the metathoracic leg (Fig. 1, *MT TH*) arises from the dorsal trachea posterior to the origin of the mesothoracic. The metathoracic also receives a branch (Fig. 1, *M T B*) from the mesothoracic trachea. The function of these short branches is not clear. They may serve as stays to hold the meso- and metathoracic tracheæ in place. Small tubes pass from the thoracics to the vertical wing muscles.

To the Wings. — Just posterior to the hinder origin of the crescent arises the anterior limb of a loop (Fig. 1, *F W*) which furnishes the fore wing with tracheæ. The posterior limb of the loop passes back and joins the dorsal connective. The posterior limbs of both the fore wing loops join the dorsal connective side by side (Fig. 1). Five tracheæ pass out from the face of the wing loop. By the successive branching of these five tracheæ the whole wing is supplied. The first or the most anterior does not bifurcate simply but sends about twenty short branches to the edge of the wing. The second and third branches are the largest and supply the greater portion of the wing while the fourth and fifth send fine branches to the posterior margins of the wing. The distribution to the hind wings is similar to that of the fore wings. There are five main tracheæ originating also from a loop whose anterior limb (Fig. 1, *H W*) arises from the mesothoracic a short distance from its origin from the dorsal. The posterior limb of the loop joins the dorsal midway between the origin of the meso- and the metathoracic tracheæ. In the larva the legs are used much more than in the adult. The wings on the other hand are functionless in the larva. Therefore it is not surprising that the tracheæ to the legs are much larger in the larva. And yet although the wings are not used there is a complex distribution to every part.

Anterior to the Stigmata. — Two pairs of tracheæ originate from the dorsal at the stigmata, an inner or cephalic pair (Fig. 1, *CEPH*) and an outer or labial pair (Fig. 1, *LAB*).

The labials (Fig. 2, *LAB*) pass alongside the cephalics for a distance, then down around the esophagus and out to the mask (Fig. 2, *M*), sending out many branches. The distribution to the mask should be noted, as this organ is in constant activity in larval life for the capture of prey. The prothoracic trachea (Fig. 1, *P TH*) arises from the labial, a short distance anterior to the stigmata.

The cephalics (Fig. 1, *CEPH*) pass along the dorsal face of the esophagus and can be traced forward to the brain. There they are connected by a loop (Fig. 1, *C L*) and from this loop five branches pass forward. The middle branch (Fig. 1, *H*) passes dorsally to the top of the head. The two pairs on each side (Fig.

1, *B*) pass forward into the brain, indicating that a considerable amount of oxygen is used in the metabolism of this organ. At the place where the loop joins the cephalic tube two branches arise together — one the optic (Fig. 1, *O*) passing out to the optic lobes (Fig. 1, *O L*) and the eyes. The other to the trophic (Fig. 1, *T*) passes down underneath the optic lobes and on out to the head parts.

Posterior Dorsals.— The dorsals give rise to branches supplying the alimentary tract — the blood vessel and reproductive organs and other adjacent tissues.

Posteriorly the dorsals become much smaller in size, this being due to the fact that each gives off many smaller tracheæ to the dorsal and lateral surfaces of the rectum (Fig. 1, *RT*). Most of these after much subdivision into fine tracheoles pass through the wall of the rectum to the rectal gills. One of the larger branches of the dorsal continues back as the post-dorsal (Fig. 1, *P D*), then passes down over the side of the rectum joining the post-ventral (Fig. 1, *P V*), which curves forward and inward on the ventral surface of the rectum connecting with the main ventral tracheal tubes (Fig. 2, *VENT*). At the place where the post-dorsal meets the post-ventral the former continues posteriorly up over the dorsal surface of the rectum (Fig. 1, *P C*).

The Ventrals. — Arising from the post-ventral the ventral tracheæ (Fig. 2, *VENT*) pass forward on the ventral surface of the rectum toward the mid line and diverge as they continue on the under surface of the stomach. At the anterior end of the stomach each ventral curves up and around crossing over the upper surface of the stomach. The right ventral finally joins the left mesothoracic trachea just beyond the latter's origin from the dorsal. Also the left ventral joins the right mesothoracic in a similar manner (Fig. *CR V*). Fig. 2 is drawn with the anterior part of the stomach removed to show the union of the ventral with the mesothoracics. It will be noted that the ventrals arising from the dorsals posteriorly join them again anteriorly. From the posterior ends of the ventrals tracheæ run to the ventral surface of the rectum and through to the rectal gills. In front where the ventrals are near together they send branches to

the malpighian tubules and furnish the greater tracheal supply to the stomach.

Lateral System. — At the posterior origin of the ventrals there arises also the lateral tracheæ (Figs. 1 and 2, *LAT*). These run anteriorly lateral to the alimentary tract and near the outer lateral edges of the abdominal walls. The laterals run forward decreasing in size and join the metathoracics just beyond their origin from the dorsals. From the lateral trachea a branch runs out externally (Figs. 1 and 2, *E AB*) to each of the first six abdominal segments supplying the muscles which assist in the compression of the abdomen. Adjacent to these tracheæ others arise from the upper face of the lateral and run to the dorsal part of each segment (Fig. 1, *S AB*). Then a third set of tracheals originate from the laterals along with the others. These the segmentals (Fig. 2, *seg*) pass ventrally along the hinder margin of each segment sending branches forwards the width of the segment. Finally a fourth set of tracheal tubes arise from the laterals in each segment, the inferior abdominal (Fig. 2, *I AB*) so named because they pass below the alimentary tract. They bifurcate a short distance from their origin from the laterals. The anterior branch (Fig. 2, *GN*) supplies the near half of the abdominal ganglion of that segment. The posterior branch (Fig. 2, *SP*) runs out to the abdominal spiracle of that segment. In the nymph as before described these spiracles are closed yet the tracheal distribution to them is clear.

The first of the ganglionic tracheoles sends a branch forwards to the metathoracic ganglion and a branch back to the second ganglionic trachea. The seventh abdominal ganglion and spiracle has a different supply receiving a branch from the posterior continuation of the dorsal (Fig. 2, *P C*). Near this arises another trachea which with a similar one from the other side forms a network in the posterior and ventral part of the body cavity. Only the main features of it are shown in Fig. 2.

The distribution to the thoracic ganglia is more complex. Each of the thoracic ganglia receives on either side a branch from the neural trachea (Fig. 2, *NEUR*). This trachea takes a somewhat tortuous course the length of the thorax alongside the thoracic ganglia. It receives a branch from the prothoracic

trachea—then just back of the mesothoracic ganglion it receives two branches, one from the mesothoracic branch (Fig. 2, *M S B*) and the other from the mesothoracic trachea itself (Fig. 2, *MS TH*). Finally the neural trachea receives two branches posteriorly. The first arises from the metathoracic branch (Fig. 2, *M T B*) the second from the metathoracic trachea (Fig. 2, *MT TH*). In addition the metathoracic ganglion as previously described receives fine tubes from the tracheæ which supply the first abdominal ganglion.

From the dorsal trachea posterior to the metathoracic there arise four tubes connecting the dorsal with the lateral trachea (Fig. 1, *D L C*). The lateral tracheæ at the anterior end are not much larger than these dorsolateral connectives.

Rectal branchiæ. — Like many of the larval dragon flies *Plathemis lydia* takes in air from the water which passes in and out of the rectum. The rectum of the nymph is proportionately much larger than in the adult. It is supplied with a complicated apparatus for separating the air from the water. The posterior end of the abdomen at the anus is provided with anal spines. There are three larger spines and a pair of smaller ones. Of the larger ones, two are ventral, one is dorsal while there is a single smaller spine between the dorsal and each of the ventrals. Just internal to these spines are three valves each adjacent to one of the larger rectal spines. The dorsal valve (Fig. 3, *D R V*) is the largest, the two ventral valves (Fig. 3, *V R V*) are of equal size. Each edge of the dorsal valve is met by the external edges of the other two, a triradiate slit being thus formed when the valves are closed.

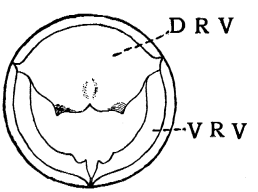

FIG. 3.

The ventral valves seem to work on the dorsal valve as a base. When the valves close water is retained in the rectum. It is forced out again by the compression of the abdomen. If it is ejected with sufficient force the animal is propelled forward in the water.

This compression of the abdomen is brought about by means of muscles connecting the roof and floor of the abdomen at its external edges. Expansion of the abdomen is due to two causes, first the relaxation of the above mentioned abdominal muscles

and second the tendency of the walls to resume their somewhat cylindrical form. Extending the length of the surface of the rectum are six longitudinal bands or muscles (Fig. 4, *RM*) a dorsal pair, a lateral pair and a ventral pair. These muscles are equally distant from each other. To each of them internally is attached two rows of leaflike structures, the rectal gills (Fig. 4, *R G*) which extend into the cavity of the rectum. The dorsal trachea (Fig. 4, *D*) sends branches to the dorsal and lateral rectal gills. From the ventral trachea (Fig. 4, *V*) branches pass to

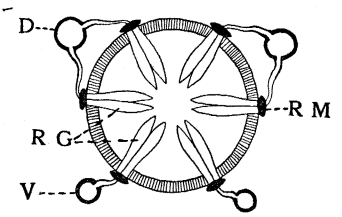

FIG. 4.

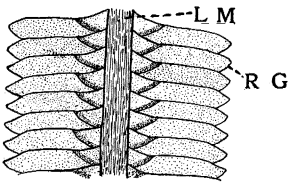

FIG. 5.

the ventral rectal gills. Fig. 5 shows the relation of the gills (Fig. 5, *R G*) to the longitudinal muscles (Fig. 5, *L M*). In this figure the gills are pressed out laterally. The shortest edge of each gill is attached diagonally to the muscle so that the lines of attachment of the two rows of gills of the same muscle have the appearance of a succession of "V's," the diverging ends being toward the posterior. Each gill is somewhat triangular in shape (Fig. 6, *R G*) the proximal edge attached to the longitudinal rectal muscles being much shorter. At one corner of this shorter side is a somewhat triangular space (Fig. 6, *TR SP*) differentiated from the rest in general appearance. Sadones '95 describes it in the gills of other species and gives no decisive clue as to the function of it. He ascribes, however, an excretory function to it.

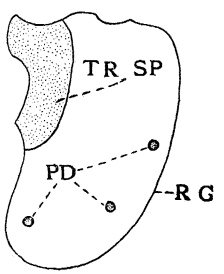

FIG. 6.

On one surface of the gill are three small pads (Fig. 6, *PD*) by which it is separated from the adjacent gills. The pads allow a thin film of water to form between each gill. Each gill is about

a millimeter in length. Oustelet, '69, estimates that there are twenty-four thousand respiratory folds in the larva of *Æschna cyanea*. These folds are not flat enough to be called gills; they are more like papillæ, but they serve the same function as gills. There are certainly as many in the rectum of *Plathemis lydia*. By the great number of folds or gills the surface area of the rectal breathing apparatus exposed to the water is increased roughly speaking about eight or ten times. As previously indicated the dorsal trachea after many subdivisions divides into two sets of tracheæ (Figs. 1 and 2, *R T*), a dorsal set and a lateral set (Fig. 4, *D*), supplying the dorsal and lateral rectal gills. The fine subdivisions of the ventrals pass to the ventral rectal gills. The final disposition of the finer tracheoles to the gill itself is shown in Fig. 7. In this figure four gills are shown teased apart. Each tracheole (Fig. 7, *G T*) bifurcates just before it reaches the upper edges of two adjacent gills of the same side. One branch (Fig. 7, *P*) passes to the posterior edge of one of the gills, while the other branch (Fig. 7, *A*) passes to the anterior edge of the gill behind. Each of these branches sends finer tracheoles into the gill. These divide and fill the gill in its most expanded portion with a network of tracheæ.

Examination under high power shows that the tracheoles (Fig. 8, *T*) from the posterior and anterior gill tracheæ form loops overlying one another (Fig. 8, *AA*). The condition in

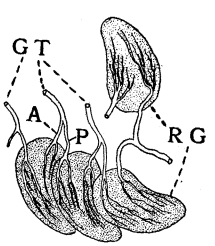

FIG. 7.

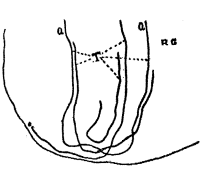

FIG. 8.

Plathemis lydia then confirms the work of Sadones, '95, who found in the Odonata he studied that the gill tracheoles were found in loops and therefore connected. A close examination of his figures, however, shows that he has drawn the tracheæ ending blindly and not in loops.

Oustelet and Palmén state that this rectal breathing apparatus does not disappear at the last ecdysis of the nymph but remains, though functionless. Hagen says that in a form he studied the whole structure disappears at that time. Whatever be the case, as far as the final moult is concerned, it is true that in the adult *Plathemis lydia* the rectal breathing apparatus has disappeared. There is indeed no further use for it since the stigmata are then functional.

The tracheal system in the nymph of *Plathemis lydia* differs in most of its details from that of *Æschna cyanea* described by Oustelet, '69. He describes four main trunks extending the length of the body and a pair of smaller abdominal tubes. These correspond to the dorsals, ventrals and laterals in *Plathemis lydia.* The four main trunks supply the rectum and respiratory papillæ in a manner roughly similar to that in *Plathemis lydia.* In *Æschna cyanea*, however, the rectal tracheæ arise from the hinder part of the dorsal at regular intervals, while in *Plathemis lydia* the hind part of the dorsal abruptly breaks up into many fine branches. The rectum of the former is furnished with respiratory papillæ, while the latter has flattened leaf-like gills. In both the tracheoles are present in loops.

In agrionid nymphs there are three long, flat caudal processes thickly supplied with tracheæ, and serve as an apparatus for taking the air from the water into the tracheal system. They are morphologically identical with the caudal spines in *P. lydia.* In the nymph of *Calopteryx*, an agrionid, there are a few internal rectal gills in addition to the three long caudal gill processes. In these forms the gill apparatus is mostly exterior. In the Æschnidæ the branchial apparatus is within the rectum. The inside surface of the rectum is provided with six longitudinal bands, each bearing a double row of folds or papillæ. In the Libellulidæ, of which *Plathemis lydia* is a member, we find not papillæ but flat processes or gills.

In the Libellulidæ there is found the highest form of the rectal gill breathing apparatus, the most specialized branchial arrangement of these three groups. On the other hand the Agrionidæ have the simplest form while the Æschnidæ have the form of branchiæ intermediate between the other two. If we were to

arrange these families according to branchial complexity we would have the following order: (1) Agrionidæ, (2) Æschnidæ, (3) Libellulidæ. And this is the order in which they are arranged by systematists. It merely indicates that the tracheal system is correlated in its complexity with the complexity of other parts, and corroborates Lubbock's statement that the tracheal system conforms to the contour of parts.

As to the phylogenetic origin of the branchial apparatus very little is known. Chun, '75, stated that Leydig had described in *Phryganea grandis* a structure which indicates that the rectal branchiæ of Libellulidæ might be considered as being developed from the rectal glands of other insects. Sharp, '95, after careful examination of Leydig's work failed to find such reference. Chun and others, however, have regarded this as the probable origin of branchiæ. Sadones, '95, after a careful examination of the evidence concludes by saying that Chun and the others who hold the above views persist in "perpetuant une notion erronée des anciens anatomistes."

In the nymph of *Plathemis lydia* the pair of thoracic stigmata between the pro and mesothorax are practically closed. When the nymph is placed in a thick solution of glycerine it invariably comes to the surface and protrudes the posterior end of the abdomen out of the fluid, the anal valves opening and closing vigorously. The caudal end always protrudes, indicating that the stigmata are not functional as yet. Hagen, '80, on the other hand believes that the thoracic stigmata are functional in the nymph. The best evidence is furnished by Dewitz, '90, who conducted a series of experiments. When the older nymphs of *Æschna* were placed in alcohol bubbles escaped from the thoracic stigmata. But in immature nymphs no gases escaped though these were subjected to a much severer test. The transition then from rectal gill breathing of the nymph to the open stigmatal type of the adult is not as sudden as ordinarily supposed, but that as the nymph grows older it gradually changes from gill breathing to the open stigmata of the adult.

When one recalls that the fine tracheoles to the rectal gills originated ultimately from the dorsal and ventral tracheæ and that these are connected posteriorly and anteriorly then it ap-

pears clear that it is hardly correct to assign the carrying of pure air to one set of tracheoles in the gill and the carrying of impure gas to the other set of tracheoles. A detailed examination of the tracheal system demonstrates not only its complexity but its many interconnections and therefore its unity. It may be regarded as the lungs of the animal whose branches ramify throughout the body, present in every tissue, carrying oxygen to every cell directly and returning the products of respiration from the tissues to the exterior. It is an arrangement admirably adapted to an organism leading a very active life — much more active than that of many of the higher forms.

G. G. SCOTT.

COLLEGE OF THE CITY OF NEW YORK.

LITERATURE CITED.

Chun.

'76 Ueber den Bau, die Entwickelung und physiologische Bedeutung der Rectaldrüsen bei den Insecten. Abh. Senckenb. Naturf., Bd. 10.

Dewitz, H.

'90 Eininger, Beobachtungen betreffend das geschlossene Tracheensystem bei Insectenlarven. Zoöl. Anz., XIII., p. 500–504, 525–531.

Hagen, H. A.?

'80 Beitrag zur Kentniss des Tracheen system der Libellenlarven. Zoöl. Anz., pp. 157–162.

Lubbock, J.

Distribution of Tracheæ in Insects. Trans. Linn. Soc., London, XXIII.

Oustelet, E.

'89 Note sur la respiration chez les nymphes des Libellules. Ann. Soc. Nat. Zöol. Ser. 5, XL., pp. 370–386.

Packard, A. S.

'98 A Text Book of Entomology. Pp. 430–484.

Palmen, J. A.

77 Zur Morphologie des Tracheensystems. Leipzig.

Sadones, J.

'95 L'Appareil digestif et respiratoire larvaire des Odonates. La Cellule, XI., pp. 271–325.

Sharp, David.

'95 Insects—The Cambridge Natural History, Vol. V. Pp. 409–429.